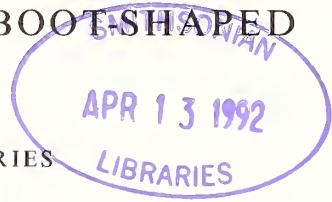


A NEW STEM-GROUP CHORDATE FROM THE LOWER ORDOVICIAN OF SOUTH WALES, AND THE PROBLEM OF LOCOMOTION IN BOOTSHAPED CORNUTES

by I. S. WOODS and R. P. S. JEFFERIES



ABSTRACT. The cornute *Procothurnocystis owensi* gen. et sp. nov., from the Upper Arenig of South Wales, is reconstructed and described. Within the chordate stem-group, it probably represents a plesion between that of '*Cothurnocystis fellinensis* Ubaghs, 1969, on the anticrownward side, and that of *Cothurnocystis elizae* Bather, 1913, on the crownward side. On death by burial, the only known specimen of *Procothurnocystis owensi* seems to have swallowed a mouthful of mud. The locomotory cycles of *Procothurnocystis owensi* and *Cothurnocystis elizae* are reconstructed, using hand-powered working models on appropriate substrates of wet clay or wet sand respectively. In its locomotory peculiarities, *Procothurnocystis owensi* probably represents the more advanced condition and *Cothurnocystis elizae* the more primitive.

THE aims of this paper are to reconstruct and describe the Welsh lower Ordovician cornute *Procothurnocystis owensi* gen. et sp. nov., to suggest its phylogenetic position and to reconstruct its locomotion along with that of *Cothurnocystis elizae* Bather, 1913.

The cornutes and mitrates are here regarded as chordates. The arguments for this view can be found in Jefferies (1986, 1990) and Cripps (1988, 1989a, 1989b, 1990).

We have reconstructed *P. owensi* from latex casts by plotting several projections simultaneously on a drawing board. Dorsal and ventral casts of the specimen were made using latex. Most of the drawings were made from these latex casts. The oral region, however, was reconstructed from an early photograph of the holotype.

PHYLOGENETIC METHODOLOGY

The terms 'total group', 'crown group' and 'stem group' still require explanation (Hennig 1969; Jefferies 1979, 1986). The total group of a monophyletic group comprises the living members of the group and all those extinct organisms which are closer related to the living members than to anything else still extant. The crown group of a monophyletic group comprises the latest species population ancestral to all the living members, and all descendants of that population, whether living or dead. And the stem group of a monophyletic group comprises all members of the total group which are not members of the crown group. A stem group is therefore paraphyletic and extinct by definition.

The stem group will consist of the stem lineage and the side branches. The stem lineage comprises all those members of the stem group which are directly ancestral to the crown group, while the side branches are descended from the stem lineage but not ancestral to the crown group. Within the stem lineage, the autapomorphies of the crown group were successively acquired. The stem group can be divided into a series of plesions, each one comprising all those organisms which, so far as can be determined, are equally closely related to the crown group (for this definition of the word plesion, see Craske and Jefferies 1989).

SYSTEMATIC PALAEOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
 Subsuperphylum DEXIOTHETICA Jefferies, 1979
 Phylum CHORDATA Bateson, 1886
 (Stem group of the Chordata)
 (Plesion of *Procothurnocystis owensi* herein)
 Genus PROCOTHURNOCYSTIS nov.

Type species. Procothurnocystis owensi sp. nov.

Diagnosis. A *Cothurnocystis*-like cornute with an x plate but no y plate, with the k-, t- and f-spikes convex-bottomed in transverse section and protruding rearwards, a horizontally flexible hind-tail, the stylocone deeply embedded in the fore-tail, two pairs of dorsal fore-tail plates corresponding to each of the 1st–4th pairs of ventral fore-tail plates, and two pairs of ventral plates (dorsal ventrals and ventral ventrals) in the 5th (most distal) fore-tail ring.

Remarks on systematic 'address'. Categorical rank for groups above the species level is arbitrary (Ax 1984, 1987; Craske and Jefferies 1989). It ought therefore to be discontinued except for the genus, which must be kept for nomenclatorial reasons. In the above systematic 'address', the traditional ranks of phylum and superphylum are quoted for the sake of completeness, while subsuperphylum is obtained by interpolation. The omission of all other categorical ranks is intentional.

Procothurnocystis owensi sp. nov.

Plate 1, figs 1–4; Plate 2, fig. 3; Text-figs 1–6, 11–12

1987 '*Cothurnocystis*' sp.; Jefferies in Fortey and Owens, p. 287, fig. 139a–b.

Etymology. This species is named in honour of Dr Robert M. Owens, of the National Museum of Wales, Cardiff, who found the only known specimen and allowed us to describe it.

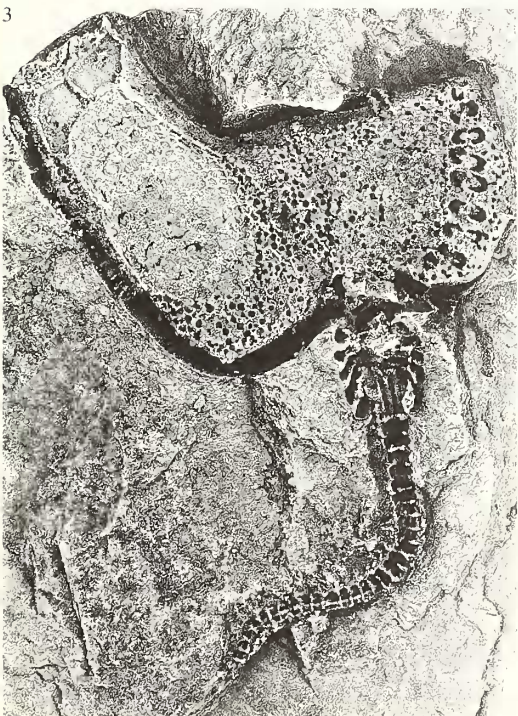
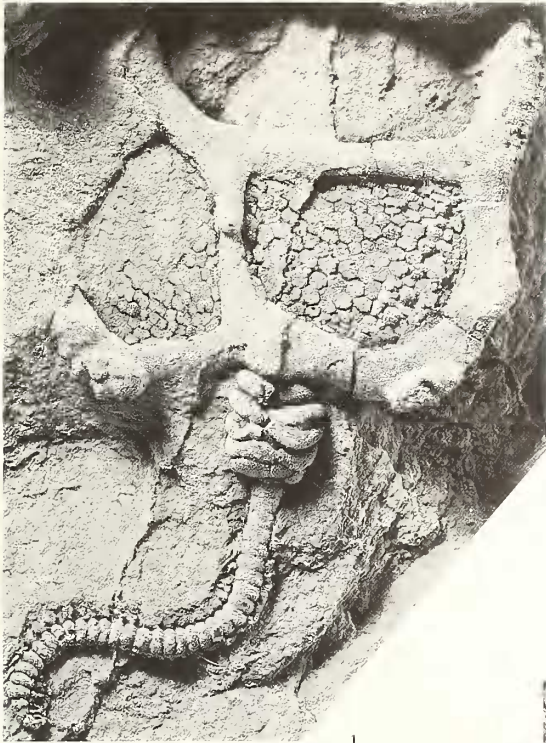
Holotype. The unique specimen is conserved in the Department of Geology, the National Museum of Wales, Cardiff, with the registration number NMW 84.17G.119. It was found in May 1979, by Dr R. M. Owens, of the National Museum of Wales, at locality 24 of Fortey and Owens (1987, p. 109; for map see fig. 2, p. 77), in the upper Arenig Pontyfenni Formation in the disused quarry near the farm of Llwyn-crwn, near the village of Whitland, Dyfed. The exact locality is at 112° and 117 m from the farm (National Grid Reference SN 2399 1795).

The specimen was preserved fully articulated and seemingly in life position. It was presumably killed by sudden burial. A last, enforced mouthful of mud can be seen in a photograph taken, shortly after discovery, at the National Museum of Wales (Pl. 1, fig. 3).

The early photograph of the specimen shows that it was almost complete when found, lacking only the anterior parts of the oral appendages (b and c). However, it has unfortunately since lost much of the oral

EXPLANATION OF PLATE 1

Figs 1–4. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; Whitland, Dyfed; Pontyfenni Fm. 1, latex cast of ventral surface, $\times 4$. 2, latex cast of dorsal surface, $\times 4$. 3, natural mould in ventral aspect, as shown by an early photograph from the National Museum of Wales; note the 'last mouthful of mud' behind the mouth, the presence of plates b, c, v and w and of a single oral spike-shaped plate near the mouth, the infilling of the gonorectal groove and sculpture of the dorsal surface of the stylocone, $\times 4$. 4, latex cast of the branchial region in dorsal aspect; the 3rd, 4th, 5th, 6th and 7th slits show a facet on the anterior U-plate for attachment of the tongue, there being no such facet on the respective posterior U-plate; the platelets of the flexible tongue are visible inside the 8th slit, $\times 16$.



region, including the stumps of b and c, the v and w plates, and much of the d plate. The damage is highly regrettable and probably results from the taking of latex casts.

Diagnosis. As for genus.

Description. See anatomical description below.

Stratigraphical occurrence. Lower Ordovician, upper Arenig, Pontyfenni Formation.

ANATOMY OF *PROCOTHURNOCYSTIS OWENSI*

An alphabetical notation (Jefferies and Prokop 1972) is used for the head plates. Plates given the same letter in different cornutes are believed to be homologous.

Procothurnocystis owensi, like all cornutes and mitrates, consists of a head and tail (Text-fig. 1A, E-F). The head is 16 mm at its widest point and the whole animal, if the tail were straightened and excluding the oral appendages (not preserved), is 29 mm long (head 14 mm, tail 15 mm). The head is asymmetrical and boot-shaped and is bordered by a marginal frame of seventeen calcite plates.

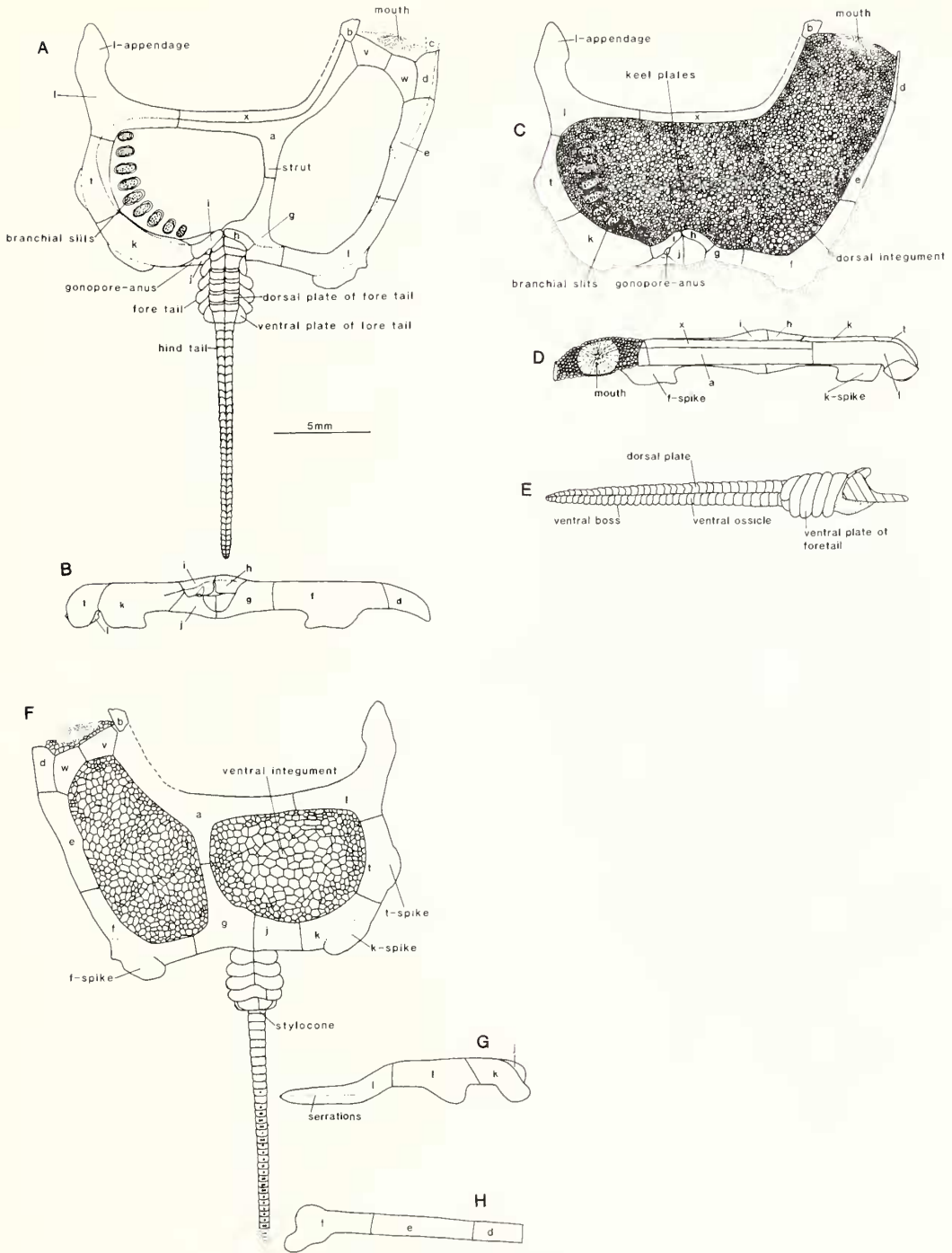
P. owensi is compared here especially with *Cothurnocystis elizae* Bather, 1913 (see Jefferies 1986, fig. 7.2a-b; Jefferies *et al.* 1987, text-fig. 14) which represents the more crownward adjacent plesion, and with '*C. fellinensis* Ubaghs, 1969 (Pl. 2, figs 1-2) which represents the less crownward adjacent plesion.

The ventral and dorsal integuments of the head of *P. owensi* were plated. As in most cornutes, the ventral integument was divided into two by the ventral strut, formed from parts of marginal plates a and g. The plates of the ventral integument were polygonal. Near the marginal frame and strut they were small and elongate, with their long axes parallel to the frame or strut, while in the middle of the two areas of integument they were larger and not elongate.

Dorsal integument. The dorsal integument was plated with numerous small plates, circular in plan view, which rarely contacted one another. A series of nine gill slits exists in the left part of the dorsal integument, near to plates t and k (Pl. 1, figs 2, 4). The smallest dorsal integument plates occur near the plates of the head frame and also around the gill slits. Their small size indicates that the integument was especially flexible in these regions. The plates in the middle of the integument are mostly larger. Some smaller plates occur between the larger integument plates and may represent newly formed plates.

There are three spines on the left part of the dorsal integument, about half way between the anterior and posterior parts of the frame (Text-fig. 1C; Pl. 2, fig. 3). The axes of the spines lie in the fossil approximately parallel to the longitudinal axis of the head. Each spine is widest proximally, pointed distally and about 1 mm long. These spines correspond in position to the left keels of the primitive cornutes *Ceratocystis perneri* Jaekel, 1900, *Protocystites menevensis* Hicks, 1872 (Jefferies *et al.* 1987) and *Nevadaecystis americana* Ubaghs, 1963 (Jefferies 1986, fig. 7.27). Presumably they represent, in some way, vestiges of such a keel. They are termed keel spines and are equivalent to the six 'épines' noted by Ubaghs (1969, p. 47) in a similar position in '*Cothurnocystis fellinensis*' (Pl. 2, fig. 2). Neither in '*C. fellinensis*' nor in *P. owensi* is there any evidence for keel spines elsewhere on the dorsal integument.

The head frame. Three spikes exist on the ventral surface of the head frame, named f-spike, k-spike and t-spike after the plates which bear them. Unlike *Cothurnocystis elizae*, the lower surfaces of the spikes are convex in transverse section rather than flat. The axis of the f-spike runs rightwards anteriorly. The spike terminates in a rounded protuberance posteriorly while anteriorly it slopes into the contours of the f plate. The k- and f-spikes are both partly visible in dorsal view. The axis of the k-spike runs leftwards anteriorly, but is otherwise similar to the f-spike. The t-spike runs



TEXT-FIG. 1. Reconstruction of *Procothurnocystis owensi* gen. et sp. nov. A, dorsal aspect without integument. B, posterior aspect of head. C, dorsal aspect of head with dorsal integument. D, anterior aspect. E, right lateral aspect of tail. F, ventral aspect. G, left lateral aspect of head. H, right lateral aspect of head, c-appendage omitted.

leftwards anteriorly, but at a smaller angle to the long axis of the cornute than either the f- or k-spikes. The posteriorly directed bosses of the k-, t-, and f-spikes in *P. owensi* are exactly contrary to the usual cornute condition of forward-pointing spikes, as seen, for example, in *Cothurnocystis elizae*.

Plate l is long, being about the same length as in '*Cothurnocystis*' *fellinensis*. It is dorso-ventrally flattened and has sharp lateral edges. There is an abrupt downward kink about 0.4 of the length from its posterior end (Text-fig. 1G), so that the anterior part lay lower than the posterior part.

There are two oral appendages (b and c). Their bases can be seen in the early photograph (Pl. 1, fig. 3) but they are incompletely preserved and their shape is therefore unknown. In the locomotory reconstructions the b and c appendages are based on those of '*Cothurnocystis*' *primaeva* Thoral, 1935 (see Ubaghs 1969, pl. 6, fig. 1).

Plate a forms the ventral part of the median anterior region of the head frame. Its posterior projection which, with part of plate g, forms the ventral strut, is relatively shorter than in '*C.*' *fellinensis* but longer than in *C. elizae*. The anterior bend in plate a of *P. owensi* is less abrupt than that of *C. elizae*.

Plate x is dorsal to plate a. In dorsal aspect, it is shaped like a reversed L, though the angle between the branches is obtuse rather than perpendicular. In having an x plate, *P. owensi* resembles '*C.*' *fellinensis* and differs from *C. elizae*.

The relative positions of plates v, w, d and c are much the same in *Procothurnocystis owensi* as in '*C.*' *fellinensis* and *C. elizae*.

A ridge runs dorso-ventrally on the inner face of plate e, somewhat anterior to the middle of the plate (Text-fig. 1A; Pl. 1, fig. 3). This ridge, and the bend in the x and a plates on the left side of the buccal lobe, probably indicate the position of the posterior border of the buccal cavity.

Plate g is constructed much as in '*C.*' *fellinensis*. Its anterior projection, to form part of the strut, is not as long or slender as the homologue in *C. elizae*.

Plates h and i in *Procothurnocystis owensi* have only a slight area of contact with each other (Pl. 1, fig. 2). Their mutually contacting surfaces are rounded, rather than being sutured as in *C. elizae*. Plates h and i have a strongly convex anterior face and a concave posterior face.

There is no plate y in *Procothurnocystis owensi*, although this plate exists between plates h and i of many cornutes such as *Ceratocystis perneri*, *Protocystites menevensis*, *Phyllocystis* spp. and '*Cothurnocystis*' *fellinensis*. The absence of plate y, and of the median eye which it always carried, is probably a synapomorphy of *P. owensi* with more crownward cornutes.

Plates g and j of *Procothurnocystis owensi* meet in the ventral mid-line of the tail insertion, as is usual in cornutes. Viewed from behind, there would be a gap between plates h, i, g and j (Text-fig. 1B). This gap connected the space inside the head skeleton with the lumen of the fore tail.

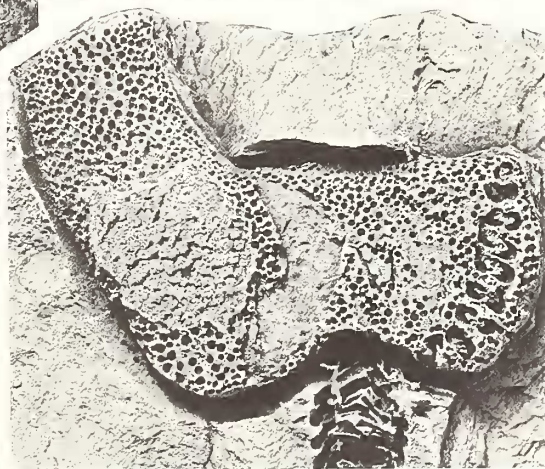
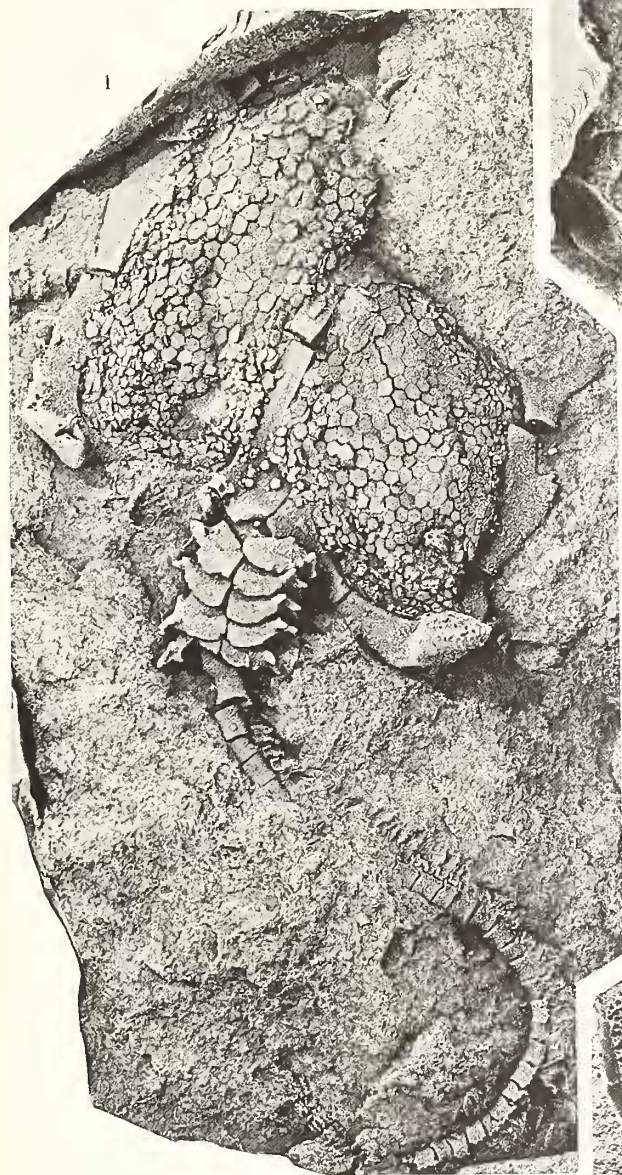
The cross-section of all the marginal plates, except the appendages, is approximately triangular – the medial face is slightly concave and is perpendicular to the convex ventral face while the third, external dorsal face links these two and is also convex. The internal faces of the marginal plates are rarely visible.

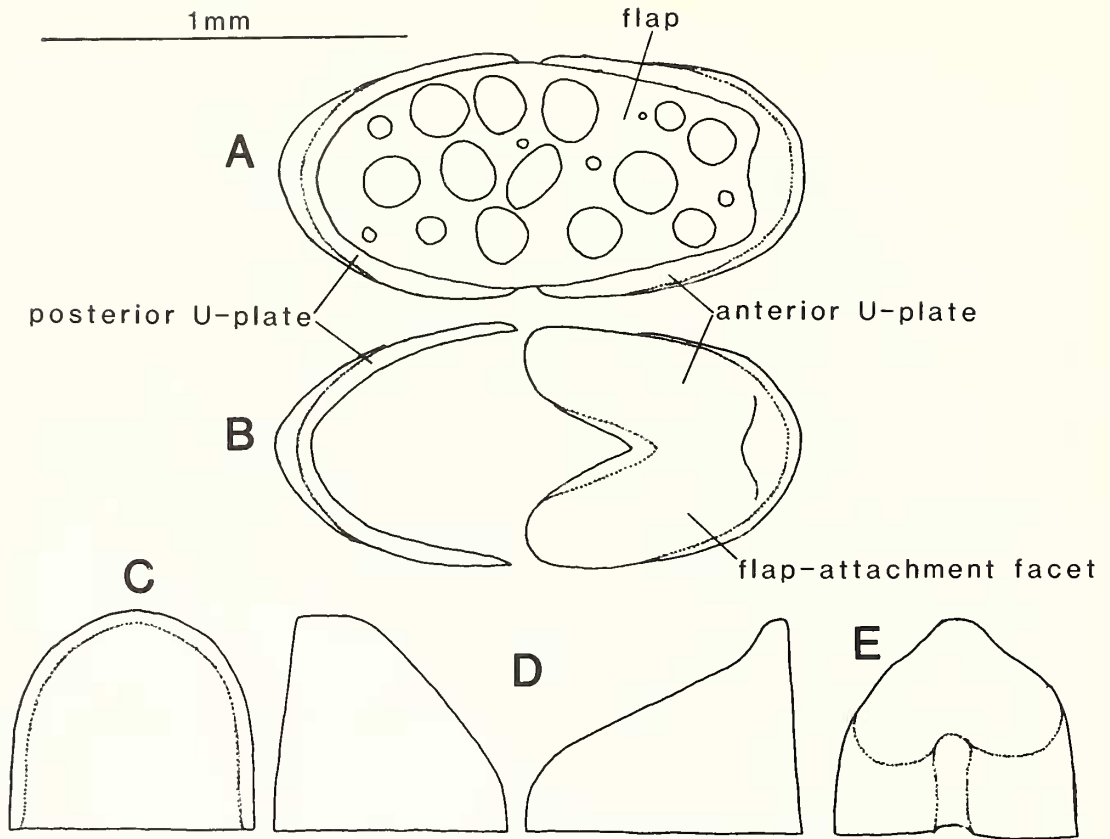
Head openings and branchial skeleton. The openings of the head are anatomically crucial. A series of nine similar openings is situated in the left, 'toe', part of the dorsal integument (Text-figs 1A, C,

EXPLANATION OF PLATE 2

Figs 1–2. '*Cothurnocystis*' *fellinensis* Ubaghs, 1969. Latex moulds of unique specimen and holotype; University of Lyon 508. 1, ventral aspect, $\times 4$. 2, dorsal aspect, note the keel spines and the curvature of the hind-tail (cf. Text-fig. 11/2), $\times 4$.

Fig. 3. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; Whitland, Dyfed; Pontyfenni Fm.; natural mould in ventral aspect in its present condition; note the three keel spines in the left part of the dorsal integument, $\times 4$.





TEXT-FIG. 2. *Procothurnocystis owensi* gen. et sp. nov. Skeleton of a gill slit. A, dorsal aspect with flap in place. B, dorsal aspect without flap. C, posterior U-plate seen from inside branchial slit. D, lateral aspect of the skeleton of a slit. E, anterior U-plate seen from inside slit.

2A-E; Pl. 1, figs 2, 4). Each of these openings is framed by an anterior and a posterior U-shaped plate of approximately equal size, which articulate with each other by touching at the free ends of the U's. There is evidence, in the form of platelets preserved within the paired U-plates (Pl. 1, fig. 4, especially the second opening from the right), that a flexible flap of integument, containing these platelets, was attached to the anterior U in life. The free end of the flap would have extended rearwards to cover the posterior U. The anterior U has a thick dorsal margin and an anterior-dorsal facet, presumably for flap attachment (Pl. 1, fig. 4, especially the 6th and 7th openings from the right). The posterior U has a considerably narrower dorsal margin, with no facet for flap attachment. These openings can readily be interpreted as outlet valves and therefore as gill slits (Jefferies 1986, p. 193).

The position of the mouth in the reconstructions, because of the above-mentioned damage to the specimen, is based mainly on the early photograph (Pl. 1, fig. 3). The latex cast and rock mould of *P. owensi* provide additional data. The early photograph clearly shows at least one plate of the oral pyramid and the positions of plates b, c, v, w and d on a natural mould mainly of the dorsal surface. This evidence of an anteriorly placed mouth is supported by an examination of the dorsal integument of the buccal region, which shows that the mouth did not open there.

A layer of rock, shown clearly in the early photograph (Pl. 1, fig. 3), separates the dorsal and ventral integuments in the region behind the mouth, but not elsewhere. This layer probably

represents a mouthful of mud, swallowed by the animal just before it died. Such a mouthful of mud suggests that *P. owensi* was a deposit feeder, taking in food particles sucked in from the topmost layer of bottom mud or the lowermost layer of water.

The gonopore–anus opens left of the tail (Text-figs 1A–C, 5A; Pl. 1, fig. 2; Pl. 3, fig. 1). The gill-slit series ends just left of the gonopore–anus, as in *Nevadaecystis americana* (see Ubaghs 1963) but unlike *Cothurnocystis elizae*. In *Protocystites menevensis* Hicks, 1872 the gonopore–anus is likewise located to the left of the tail. In the reconstruction of this species given by Jefferies *et al.* (1987) the gill-slit series is shown as extending in front of the gonopore–anus, as in *C. elizae*, but it does not in fact do so, as shown by examining text-figures 10a and 15 and plate 54, figure 1 of that paper. The situation in *P. owensi*, with the gill-slit series stopping just left of the gonopore–anus, being thus found in the anti-crownward plesions of *N. americana* and *P. menevensis*, is probably primitive compared with the condition in *C. elizae*.

Chambers and soft anatomy of the head. Because of the preservation of the fossil, only a limited amount can be said about the internal soft anatomy of the head.

The buccal cavity would be bounded, posteriorly on the left, by the abrupt bend in the a and x plates and, posteriorly on the right, by the almost vertical ridge running down the medial face of the e plate.

The position of the posterior coelom can be inferred only by comparison with *C. elizae* and other cornutes. The infilling of the gonorectal groove can be seen crossing the posterior coelom in the early photograph (Pl. 1, fig. 3), but no other internal features are visible in this region.

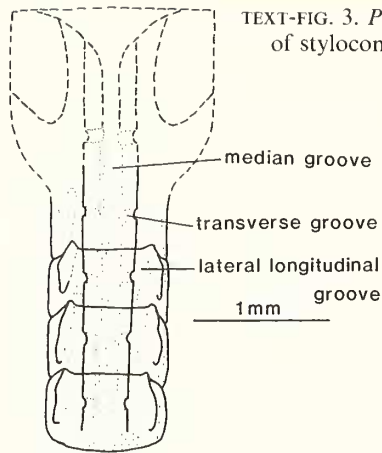
The pharynx was probably the largest chamber in the head. Towards its left end, the row of nine gill slits presumably opened through its roof.

The ridge on the internal mould which represented the infilling of the gonorectal canal is shown to enter the region of the posterior coelom from anterior right in the early photograph of the specimen (Pl. 1, fig. 3). This suggests that the patent part of the right anterior coelom, which would have contained the gonad and most of the non-pharyngeal gut, lay in its invariable cornute position, in the posterior right part of the head (the 'heel' part of the 'boot').

Attachment of the dorsal integument. The dorsal integument would be attached near the upper edge of the medial face of the marginal plates. On some plates, such as x and t, a narrow, horizontally elongate groove is seen at the top of the approximately vertical medial face, and this groove is probably an attachment facet for the dorsal integument. On plates k, i and h, however, the same groove passes onto the dorsal surface of the plates. In the only known specimen, the dorsal integument is still largely attached to the frame but has been pushed down into the head by the weight of overlying sediment. Thus most of the medial face of the marginal plates is obscured by the dorsal integument.

The tail. The tail of *P. owensi* is well preserved in both dorsal and ventral aspect (Text-figs 1A–H, 3–6; Pl. 1, figs 1–3).

The skeleton of the fore-tail (Text-fig. 5) is complicated and differs considerably from the condition normal to cornutes as represented by *Cothurnocystis elizae* for example. Such normal forms show a number of imbricating rings, each comprising a symmetrical pair of large ventral plates and a symmetrical pair of smaller dorsal plates. In *Procothurnocystis owensi*, the fore-tail plates are similarly arranged in rings, there being five such rings altogether. The first three rings are normal, except that there are two pairs of dorsal plates for each ring (Pl. 3, fig. 1), instead of one pair. Probably the anterior pair in each ring, which are much larger than the posterior pair, are homologous with the dorsal plates of other cornutes, whereas the posterior pair represent an autapomorphy of *P. owensi*. The ventral plates of each of these three rings are sutured together in the mid line, while the dorsal plates are not sutured medially but meet at a rounded edge. The ventral plates of the first three rings form, in transverse section, about three-quarters of the circumference of the tail, the remaining quarter being formed from the dorsal plates.



TEXT-FIG. 3. *Procothurnocystis owensi* gen. et sp. nov. Reconstruction of stylocone and of the first hind-tail ossicles in dorsal aspect.

The fourth ring is like the first three, except that the suture between the two ventral plates is left of the midline (Pl. 3, fig. 2; Text-fig. 5C-D).

The fifth ring is different. There is a single pair of dorsal plates, as usual in cornutes, rather than two pairs (Pl. 3, fig. 1). And, on the other hand, there are two pairs of ventral plates, i.e. dorsal ventral plates, and ventral ventral plates (Pl. 3, fig. 2; Text-fig. 5C-D).

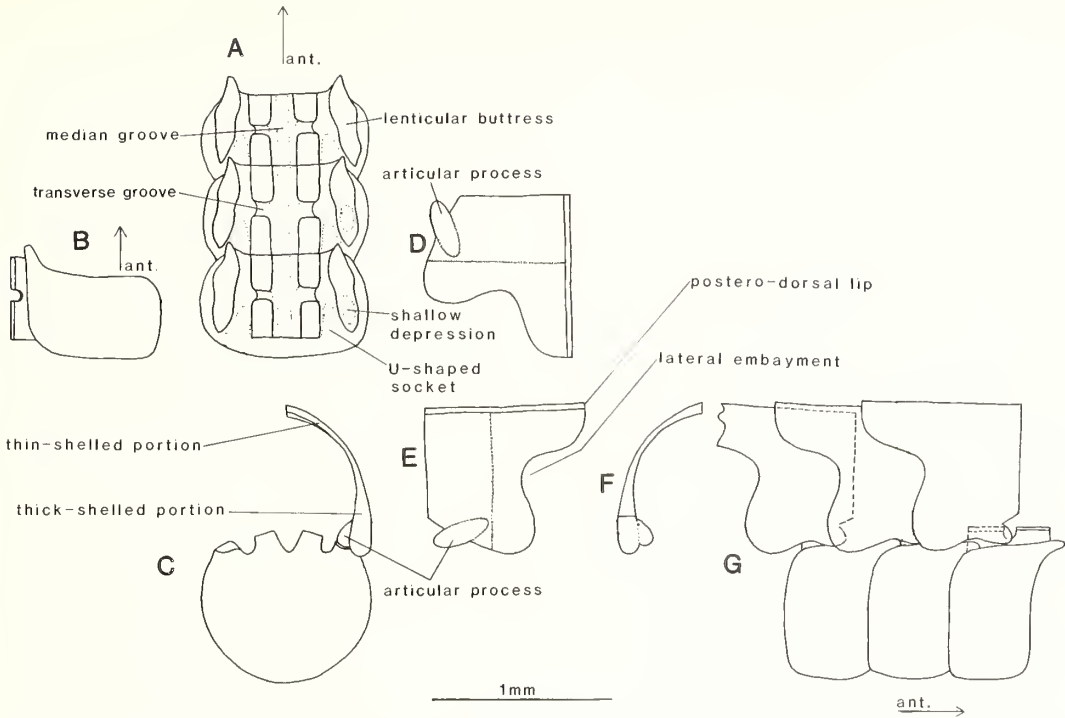
Concerning other points in the fore-tail anatomy, at the front end of the fore-tail two pairs of plates fill the gap between the first ring and plates h and i (Text-figs 1A, 5A-B; Pl. 1, fig. 2). Each fore-tail ring imbricates over its more posterior neighbour. Ventrally the posterior margin of the ventral plates points anteriorly in the midline. In lateral view the posterior margin of the ventral plates is convex posteriorly. Altogether, there are eleven pairs of imbricating dorsal plates in the fore-tail and this is about double the usual number of dorsal plates as seen in *C. elizae* or '*C. fellinensis*'.

As discussed below, the fore-tail has the stylocone deeply inserted into it and the anterior excavation of the stylocone is very shallow. For both these reasons, there would have been very little space inside the fore-tail for muscle (see Text-figs 1A, E-F, 3; Pl. 1, figs 1-3).

The structure of the fore-tail is suited to dorso-ventral flexion in its anterior part, i.e. in front of the anterior end of the deeply inserted stylocone. The dorsal plates are particularly adapted to allow ventral flexion, since their large numbers would allow the dorsal surface to stretch. The posteriorly convex shape of the ventral plates in lateral aspect (Text-fig. 1E) would allow them to flex in a vertical plane.

The stylocone of *P. owensi*, as mentioned, is deeply inserted into the fore-tail – only about one tenth of its length would have been visible from outside when the animal was alive (Pl. 1, fig. 3). This deep insertion is unique among cornutes. The stylocone is vase-shaped, with a slim stem posteriorly and the greatest breadth anteriorly (Text-fig. 3). It overlies the ventral parts of the three most posterior rings of the fore-tail and is itself overlain by the dorsal plates of these three rings. A single pair of dorsal plates, immediately posterior to the fifth ring of the fore-tail, articulate with the stylocone.

The sculpture of the dorsal surface of the stylocone is shown in the early photograph (Pl. 1, fig. 3; Text-fig. 3) and confirmed, in part, by the latexes and specimen in their present state. There is a median groove, believed to have contained the notochord. From this groove in the stylocone extend two pairs of transverse grooves. The precise outline of the stylocone is doubtful. The early photograph shows a pair of large but shallow lateral excavations situated antero-laterally on the dorsal surface of the stylocone. As already said, the anterior median excavation of the stylocone



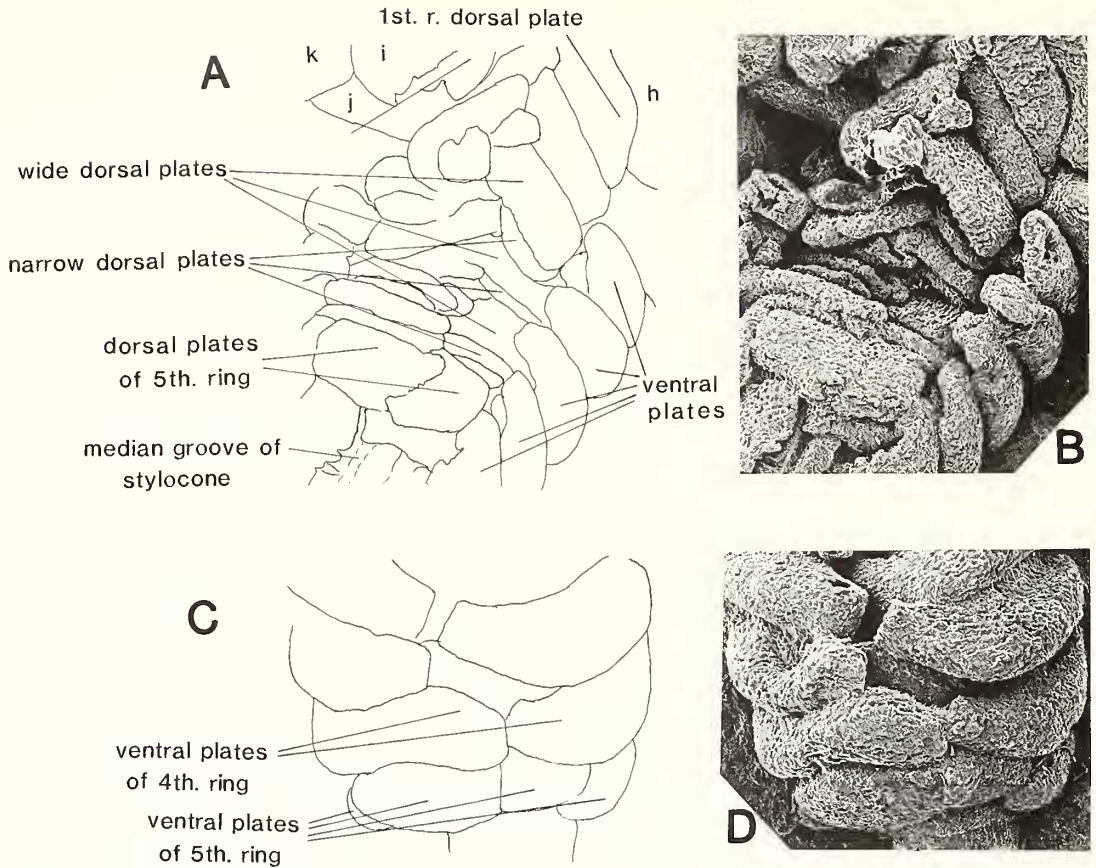
TEXT-FIG. 4. *Procothurnocystis owensi* gen. et sp. nov. Anatomy of the hind-tail. A, dorsal aspect of three hind-tail ossicles. B, right aspect of a hind-tail ossicle. C, posterior aspect of a hind-tail ossicle and of right dorsal plate in life position. D, medial aspect of plate rotated transversely from its life position without movement anteriorly or posteriorly. E, medial aspect of the same plate in its life orientation, rotated 90° from its position in C. F, anterior aspect of the same plate. G, right lateral aspect of three ossicles and three plates.

seems to have been much shallower than in other cornutes. This is shown by the same photograph (Pl. 1, fig. 3).

The hind-tail consists of thirty-five segments. The skeleton comprises ventral ossicles and paired dorsal plates meeting in the midline.

There is one ventral ossicle in each segment of the hind-tail. The sculpture of the dorsal surfaces of the ossicles can be seen in several places (Text-figs 4A, 6; Pl. 1, fig. 2). It consists of a median groove with a pair of ill-defined longitudinal lateral grooves to left and right of it in each ossicle. From the median groove, a pair of transverse grooves run out in each ossicle, to open into the lateral grooves. The longitudinal lateral groove shows a slight deepening at the end of each transverse groove. At the posterior end of each longitudinal lateral groove in each ossicle there is a shallow U-shaped excavation. Lateral to the lateral groove there is a slightly raised lenticular facet, running approximately parallel to the median groove but diverging slightly outwards and rearwards. For each ossicle, the anterior end of the lenticular facet is carried forward as the dorsal surface of an articulation horn and projects somewhat into the U-shaped excavation of the next ossicle in front (Text-fig. 6A-B). Towards the posterior end of the lenticular facet is a shallow elliptical depression, which presumably articulated with an articular process seen on the dorsal plate (Text-fig. 6C-D). The proximal ventral ossicles are roughly semicircular in transverse section whereas more distal ossicles are wider relative to their depth.

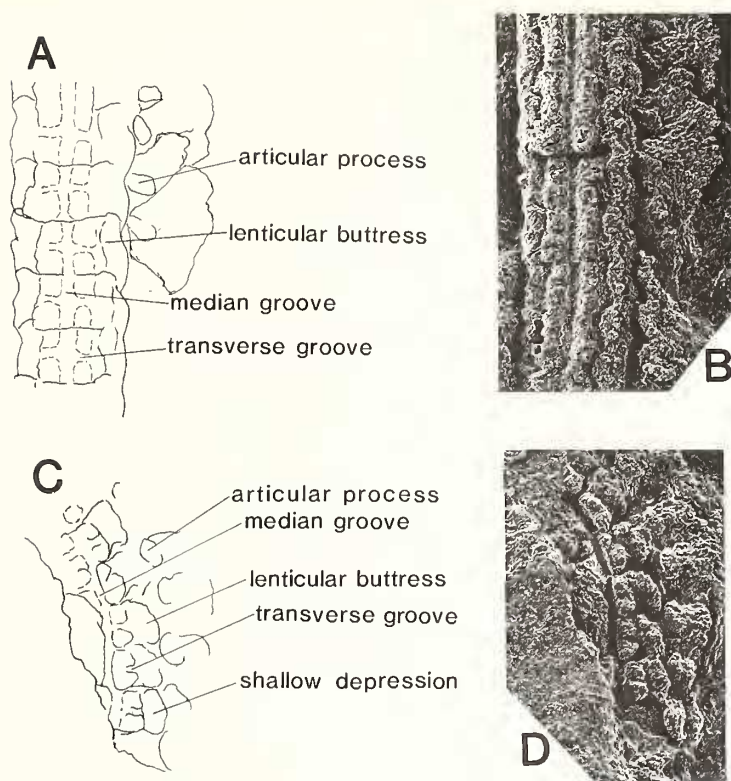
Thus the ossicles articulate together. The nature of this articulation is that, on right and left, an anterior lateral horn (which bears on its dorsal surface the anterior end of a lenticular facet) projects



TEXT-FIG. 5. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; scanning electron micrographs (B, D) and explanatory sketches (A, C) of latex casts of fore-tail; all figures $\times 15.4$. A–B, dorsal aspect; C–D, ventral aspect.

into the shallow U-shaped excavation in the next ossicle anterior (Text-fig. 4A–B, G). The shape of the anterior horns of each ossicle, and their articulation with the next ossicle in front, suggest that a little flexing may have occurred in the vertical plane. However, it is clear from the shape of the ossicles and dorsal plates, and from the posture of the fossil as preserved, that the more distal portion of the tail (ossicles 9–35) could flex much more strongly in the horizontal plane than vertically. The preservation of the fossil also suggests that the hind-tail corresponding to ossicles 1–9 was probably almost rigid in all directions. The junctions between the more proximal ossicles were planar (except for the articulation horns) but it was difficult to assess the curvature of such junctions more distally. In the series of ossicles from 9 to 35 it seems that the tip of the tail could probably be flexed in the horizontal plane through a total of 180° or more, as indicated by the preserved posture of the hind-tail in the fossil (Pl. 1, figs 1–3).

The ventral face of each of the more posterior ossicles is developed as a broadly convex ventral boss. From ossicle 11 rearwards most ossicles have, in addition, small rounded protuberances, usually one but sometimes two, on or near the ventral midline (Text-fig. 1F; Pl. 1, fig. 1). Presumably the ventral bosses and protuberances helped to grip the substrate during locomotion. The protuberances may be homologous with the ventral spikes of more crownward cornutes, e.g. *Reticulocarpos hanusi* Jefferies and Prokop, 1972.



TEXT-FIG. 6. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; scanning electron micrographs (B, D) and explanatory sketches (A, C) of latex casts of hind-tail in dorsal aspect; all figures $\times 15.4$; B, proximal portion; D, distal portion; cf. Pl. 1, fig. 2.

The last four ossicles of the tail decrease progressively in size, so that the width of the last ossicle (No. 35) is approximately 0.4 the width of the fourth from last ossicle (No. 32). Furthermore, the last ossicle appears to be rounded. Hence *P. owensi* has a definite terminal ossicle. This is contrary to the assertion in Jefferies (1986, p. 193) that the end of the tail in cornutes is always abrupt.

The dorsal plates (Text-figs 4C–G, 6; Pl. 1, figs 1–2) consist of a thin-shelled dorsal portion and a thick-shelled ventral portion. The thick-shelled portion had, in lateral aspect (Text-fig. 4D), a convex posterior margin, forming a ventral lobe which overlapped the next plate posterior, while more dorsally the margin of the plate was at first concave in lateral aspect (the lateral embayment) and then convex again at the midline (forming with its antimere a median postero-dorsal process). The lateral embayment, being situated where the tail in transverse section is widest, would allow considerable horizontal flexion while the median postero-dorsal process would tend to prevent dorsal flexion. (This is particularly the case because the median dorsal suture between a pair of plates was long, extending the length of two ossicles.) The anterior margin of each plate was approximately straight in lateral aspect. The dorsal plate was half-U-shaped in posterior aspect so that, when the dorsal plates were paired in life, the inverted U would be complete. The ventral articulation of each dorsal plate is somewhat longer than the ventral ossicle with which it mainly articulates. On the inside of the anterior ventral region of each plate was a boss-like articular process which articulated with the elliptical depression on the lenticular facet of the ventral ossicle. The position of the boss and depression means that each plate overlapped the next posterior plate and

that each plate extended onto the next ossicle behind. The wall of each plate was thicker anteriorly than posteriorly to allow for imbrication with the next plate.

LOCOMOTION

The strange shape of boot-shaped cornutes raises the question of whether they moved and how. Jefferies (e.g. 1986, p. 104) has suggested that, like all calcichordates, they crawled rearwards across the sea floor, pulled by their tails.

In reconstructing possible locomotory cycles for *Cothurnocystis elizae* and *Procothurnocystis owensi*, we first take *C. elizae*. Features probably important in its locomotion are stressed in Text-figure 10 (tail, k-spike, t-spike, l-appendage, b-appendage, c-appendage, f-spike). We recall that spikes by definition are short and ventrally directed, whereas appendages are elongated and directed anteriorly. A rearward direction of locomotion is suggested by the fact that the t-, k- and f-spikes have points or sharp edges anteriorly but blunt ends posteriorly, while the l-, b- and c-appendages slope downwards and forwards. The l- and b-appendages were rigidly fixed to the head, whereas the c-appendage, right of the mouth, was articulated to the marginal frame and would have been able to wag to right or left. The mere left-right asymmetry of the head of *C. elizae* is consistent with rearward locomotion, since asymmetrical objects are directionally stable if pulled, but not if pushed.

The fore-tail of *C. elizae* was adapted to flex laterally, as shown by gaps between the successive rings of major plates of the fore-tail on the right and left but not in the ventral or dorsal midlines. Also the distal half or third of the hind-tail of *C. elizae* seems, because of the horizontally cylindrical junctions between some of the ventral ossicles, to be adapted for bending downwards (Jefferies 1986, p. 202). Such downward flexure would be passive and would result from the elasticity of ligamentary fibres joining the ventral hind-tail ossicles. Straightening of the hind-tail would be an active process, caused by the contraction of muscles in the lumen of the hind-tail. A specimen of the hind-tail of *C. elizae* preserved with the postulated downward terminal flexure is shown in Text-figure 7F.

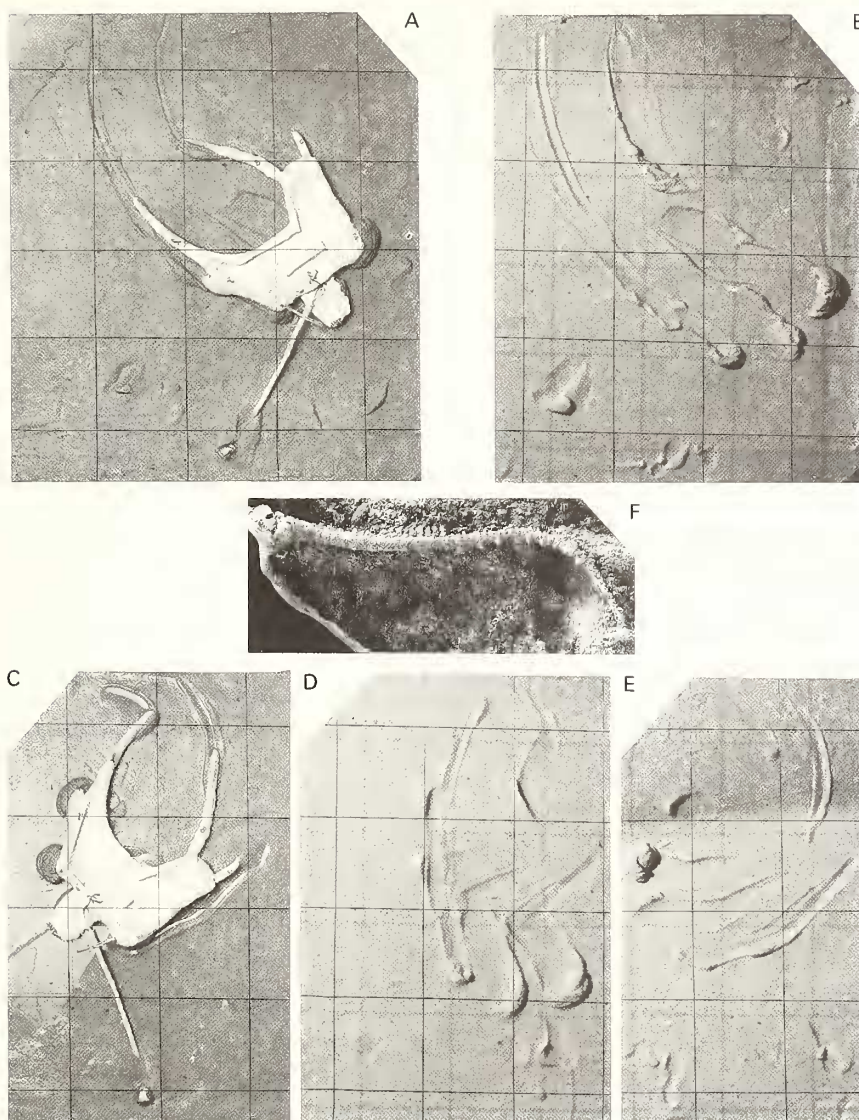
We made a model so as to reconstruct experimentally the locomotory cycle of *C. elizae* (Text-fig. 7A, C). It was about nine times natural size. The head and fore-tail were fashioned from wood and hard-setting resin. They were modelled in three dimensions and were accurate as concerns the ventral and lateral surfaces. The mid- and hind-tail were of stiff plastic-wrapped wire. They were loosely hinged to the head at the tail insertion – in shape the hind-tail curved ventrally in a distal direction, as it probably could in *C. elizae* in life. At the very tip of the tail there was an upwardly directed handle which did not exist in the animal but was experimentally convenient. An imperfection in the model was that the small c-appendage, right of the mouth, was rigidly fixed to the frame, rather than being able to wag to right and left as in the living animal.

We caused the model to locomote across the planar horizontal surface of some water-saturated sand in a shallow square box (Text-fig. 7). When placed on the sand, the model rested on the flat lower surfaces of the spikes and the lower surfaces of the appendages and tail. The ventral integument did not touch the sand.

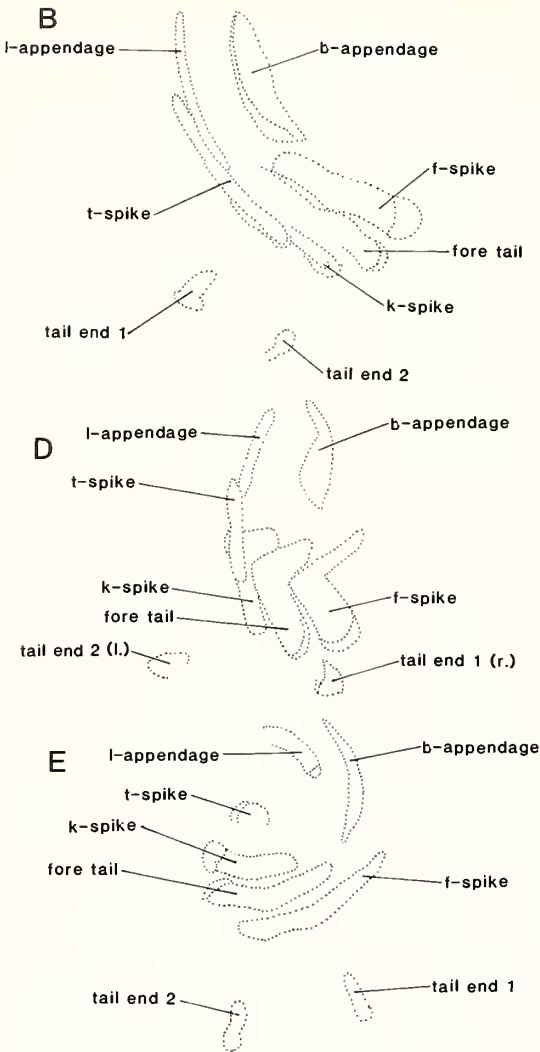
To produce the appropriate movement, the experimenter held the distal end of the tail into the sand by the vertical handle, while pushing gently sideways with one finger on the proximal end of the wire which represented the mid- and hind-tail. By these actions he imitated the ventralward hooking of the distal part of the tail to grip the substrate and the contraction of the left or right fore-tail muscles.

A four-stroke locomotory cycle was worked out using the model of *C. elizae* (Text-figs 7–9). It comprised: (1) a tail-leftward power stroke (Text-fig. 9A); (2) a tail-rightward return stroke; (3) a tail-rightward power stroke (Text-fig. 9B); and (4) a tail-leftward return stroke.

Going into more detail, the cycle starts with the tail-leftward power stroke. The distal part of the hind-tail was inserted into the sediment at the midline and the fore-tail then flexed to its maximum leftward extent, relative to the head (Text-fig. 7A). As mid- and hind-tail thus swung leftward and forward relative to the head, the head yawed anti-clockwise relative to the sea floor, about a region centred anterior to and right of the head. The tracks made by the model in two successive tail-left



TEXT-FIG. 7. *Cothurnocystis elizae* Bather, 1913. A–E, experiments on locomotion; the sides of the grid squares are 100 mm long and the model is about $9 \times$ natural size; for explanation of individual tracks in B, D and E, see Text-figure 8. A, model lying on wet sand after two successive tail-left power strokes – note the piling-up of sand at the f-spike, and to a lesser extent at the k-spike, and the tracks caused by sliding along the l-appendage and by moving perpendicular to the b-appendage. B, tracks after two successive tail-left power strokes. C, model at end of a single tail-right power stroke – note the piling-up of sand at the k- and t-spikes, and the tracks caused by sliding along the b-appendage and by moving perpendicular to the l-appendage. D, tracks after a tail-right power stroke followed by a tail-left power stroke. E, tracks after two successive tail-right power strokes. F, latex cast of specimen BMNH E23197 (Gray Collection) from the type locality of the species, i.e. the Starfish Bed of Harper's (1982) Locality 6, near Girvan, Scotland (Upper Rawtheyan Stage of Ashgill Series), $\times 1.8$; the specimen, in left lateral aspect, shows part of the fore-tail, and the entire mid- and hind-tail, preserved with the sagittal plane parallel to the bedding; the curvature is probably natural and resulted from elastic contraction of ligamentary fibres in the ventral column of ossicles when the dorsal muscles relaxed at death – note the ventral protuberances in the anterior part of the distal half of the hind-tail and the down-turned end of the hind-tail.

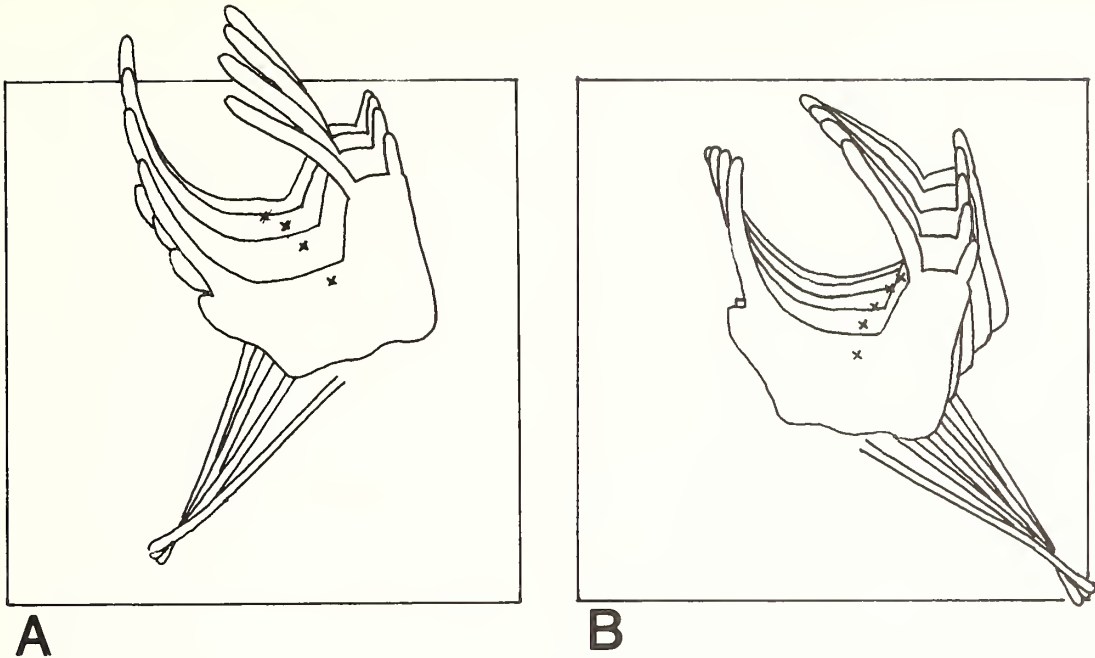


TEXT-FIG. 8. *Cothurnocystis elizae* Bather, 1913. Tracings to explain the tracks shown in Text-figure 7 A-E. The tracings take the same letters as the corresponding figures in Text-figure 7.

power strokes (Text-fig. 7B) show that: (1) sediment piled up behind the f-spike on the right posterior corner of the head, and to a lesser extent behind the k-spike on the left side of the head; (2) the t-spike (likewise on the left) slid rearwards over the substrate; (3) the curved l-appendage (on the extreme left of the head) slid rearwards along its length in the manner of an arcuate sledge runner or ski; and (4) the b-appendage, which was curved in the opposite direction to the l-spike, slid over the sand while rotating leftward and rearward transversely to its own length. Piling-up of sediment shows where the substrate was resisting movement of the head.

In the tail-rightward return stroke, the mid- and hind-tail would swing, entirely in water and without gripping the sea floor, from its extreme left position to the midline.

The tail-right power stroke began when the distal part of the hind-tail was inserted into the sea bottom at the midline. The fore-tail then flexed to its maximum rightward extent, relative to the head (Text-fig. 7C). As a result, the head yawed clockwise, relative to the sea floor, around a centre near the left side of the head at the proximal end of the l-appendage. Tracks made in two successive



TEXT-FIG. 9. *Cothurnocystis elizae* Bather, 1913. Successive positions of the head and tail during the power strokes of the locomotory cycle. Drawings traced from photographs of the model – compare Text-figures 5 and 6; the side of the square represents 300 mm in the model and about 33 mm in life; x marks estimated position of centre of mass of the head. A, tail-left power stroke. B, tail-right power stroke.

tail-right power strokes (Text-fig. 7E) show that: (1) sediment would pile up on the left side of the head against the k-spike and the t-spike; (2) the curved b-appendage would slide rearwards along its own length as an arcuate sledge-runner; (3) the f-spike and the c-appendage (both on the right side of the animal) would slide clockwise over the sediment; and (4) the l-appendage, being curved in the opposite direction to the b-appendage, would rotate rightwards, sliding over sediment transversely to its own length.

In the tail-leftward return stroke, the tail would swing, entirely in water and without gripping the sea floor, from its extreme right position to the midline. The locomotory cycle would then start again.

The c-appendage, as already mentioned, was articulated to the frame in the animal (Text-fig. 10), but not in the model. In life it could probably take up two different positions. Namely, it would wag passively to the right during the tail-leftward power stroke, so that its length was concentric to the curvature of the l-appendage (along which the head was then sliding), and would wag passively to the left during the tail-right power stroke, so that its length was concentric to the curvature of the b-appendage (along which the head was then sliding). By so wagging, it would always present least resistance to the rearward motion of the animal by sliding rearward along its own length. This view of the function of the c-appendage seems more elegant and likely than the opinion of Jefferies (1968, p. 258) who thought that, by waving actively from side to side, it served to stir up the food-rich bottom mud which then would be sucked into the mouth as a suspension.

To generalize, each ventral spike alternated in its mode of action during successive, opposite-sided power strokes – namely it would grip the sea floor strongly during one power stroke and grip it more weakly or slide rearwards over it in the next. Likewise the l and b appendages alternated in their action, sliding rearwards along their curved length in one power stroke and rotating

transverse to their length in the next. The l-appendage and the k- and t-spikes (on the left side of the head) would show one of these modes of action during any one power stroke, whereas the b-appendage and the f-spike (more on the right side of the head) would show the other. The small, articulated c-appendage would, by passive drag, take up one of two alternative positions, so as to resist rearward motion as little as possible.

Speaking quantitatively, we estimated the position of the centre of mass for the head of *C. elizae* by suspending a cardboard silhouette of the head from various hinge points. It probably lay anterior to the midline of the tail insertion, shortly behind the anterior frame, as indicated in Text-figure 9. We measured the motion of the centre of mass during a locomotory cycle on the basis of successive photographs taken of the model lying on the wet sand. If the length of the head is measured from the anterior end of the b-appendage to the midline of the tail insertion, then the centre of mass moved rearwards by 70% of the head length during the total cycle. This rearward translation happened in two equal phases: during the tail-leftward power stroke, the centre was translated 20% of the head length to the right and 35% of the head length rearwards; and during the tail-rightward power stroke, it was translated 20% of the head length to the left, and 35% of the head length rearwards. During each power stroke, the hind-tail wagged through 30° relative to the sea floor, and through 50° relative to the posterior margin of the head frame. Consequently, the posterior margin of the head rotated, relative to the sea floor, 20° during each power stroke – anti-clockwise during the tail-left stroke, and clockwise during the tail-right stroke. (All measurements given are approximate.) Thus in terms of the total movement of the head, whether in translation or rotation, the tail-left and tail-right power strokes were mirror images of each other.

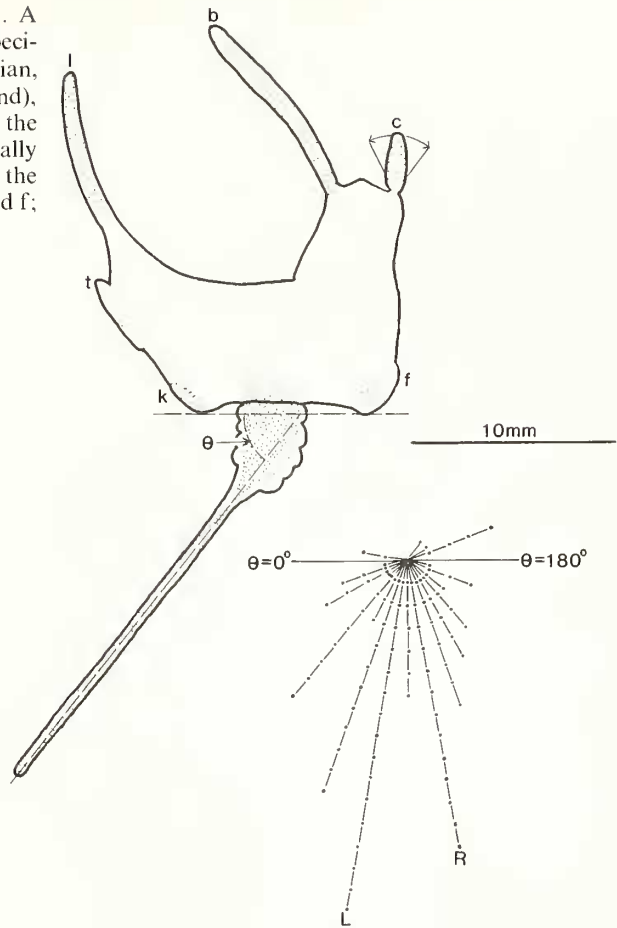
Jefferies (1969, p. 525) recorded the position of the hind-tail relative to the head in ninety-six specimens of *C. elizae* from the Starfish Bed at Girvan (Text-fig. 10). He found that there were two specially frequent positions, situated approximately 10° right of the midline (thirteen specimens) and 10° left of it (sixteen specimens). These positions would correspond, respectively, to the beginnings of the tail-rightward and tail-leftward power strokes. In six specimens the hind-tail extended (to within 10°) exactly rearwards from the midline of the tail insertion. In forty-one specimens it was 5° or more left of the midline; and in forty-nine specimens it was 5° or more right of the midline. These data represent the postures of animals at death by burial. They suggest that the tail-leftward and tail-rightward power strokes were about equally frequent and that the animals tended to die at, or shortly after, the start of a power stroke, presumably because oxygen consumption was highest then.

If this was how *Cothurnocystis elizae* moved, it would have made tracks on the sea floor like those in Text-figure 7. It would be miraculous if such tracks were ever found, however. The fact that so many features of the anatomy of *C. elizae* can be explained by the postulated mode of locomotion, suggests that it really did move in the manner suggested.

Turning to *Procothurnocystis owensi*, the tail, as already mentioned, had several striking features: (1) the posterior part of the hind-tail, approximately distal to ossicle 10, could flex horizontally but probably not, or almost not, vertically; (2) the anterior part of the hind-tail, approximately as far back as the 10th ossicle, probably could not flex in any direction and the same was presumably true of the posterior part of the fore-tail, for in it the stylocone was deeply inserted; (3) the anterior part of the fore-tail could probably flex vertically but not, or almost not, horizontally; and (4) there was little space for muscles in the fore-tail, since the stylocone was deeply inserted into the fore-tail and had a very shallow anterior excavation. The small size of any fore-tail muscles suggests that in *P. owensi*, unlike *C. elizae* and probably most other cornutes, they were not the main motor in locomotion.

The head of *Procothurnocystis owensi* also shows peculiar features. Namely, the tips of the t, k and f spikes project rearwards instead of forwards, and thus in the opposite direction to those of all other known cornutes, and the lower surfaces of the spikes are convex in transverse section rather than flattened. The f- and k-spikes are almost mirror images of each other. Both these spikes are elongate, their long axes converge rearwards and there is an angle of about 70° between the long axis of the fore tail and the long axis of the spike.

TEXT-FIG. 10. *Cothurnocystis elizae* Bather, 1913. A census of observed tail positions in ninety-six specimens from the type locality (upper Ordovician, Ashgill Series, Thraive Glen, near Girvan, Scotland), redrawn and modified after Jefferies (1969); the animal is shown in dorsal aspect but ventrally prominent parts of the head and buried parts of the tail are stippled. Ventral spikes are labelled t, k and f; appendages are labelled l, b and c.



Horizontally flexible hind-tails, revealed by the posture of the animals at death by burial, are known in some other cornutes. Such include '*Cothurnocystis*' *fellinensis* Ubaghs, 1969, *Thoralicystis melchiori* (Ubaghs, 1983) (see Cripps 1988) and *Scotiaecystis collapsa* Cripps, 1988. Wherever observed, this horizontal flexibility is perhaps homologous. Predominantly vertical flexion of the fore-tail on the other hand, is deduced to have occurred in crownward cornutes such as *Reticulocarpos hanusi* Jefferies and Prokop, 1972, and in mitrates. In these forms it is not likely to have been homologous with vertical flexion in the fore-tail of *P. owensi*.

The horizontally curved shape of the hind-tail (Pl. 1, figs 1–3), in the fossil as preserved, from ossicle 10 to ossicle 35, represents about half a wavelength of a sine wave. Probably the posterior part of the hind-tail, as it flexed from side to side, would pivot about the ninth ossicle. Sine waves would pass forward along this laterally flexible region by muscular contraction and relaxation.

We made a scale model of the head of *Procothurnocystis owensi*. It was about eight times natural size and constructed, like the model of *Cothurnocystis elizae*, of wood and hard-setting resin. The shapes of plates b and c in the model were based on those of '*Cothurnocystis*' *primaeva* Thoral, 1935. We did not attempt to model the tail because its mode of action was probably very complicated.

We caused the head to locomote across the surface of water-saturated clay in a shallow square box by placing one finger on the rear part of the head frame and pressing obliquely rearwards and

towards the midline, alternately co-linear with the f-spike on the right or with the t- and k-spikes on the left. The clay was intended to simulate the very soft clayey mud on which *P. owensi* probably lived and died. Unlike *C. elizae*, the head did not rest on the ventral surface of the spikes, but sank down so that the ventral integument and strut rested on the clay while the spikes, much of the l-appendage and the whole of the b- and c-appendages were embedded within it. (We recall that the shapes of the b- and c-appendages are unknown.) Pressing rearwards on the frame in the manner described produced rearward movement with much yaw. Thus, when pulled at the right towards the rear and leftwards, the head would slide readily along the length of the f-spike, while tending to pivot about the k- and t-spikes on the left side of the head. The result was rearward translation and clockwise rotation. When pulled at the left towards the rear and rightwards, the head would slide readily along the common axis of the k- and t-spikes, pivoting about the f-spike on the right side of the head. The result was rearward translation and anti-clockwise rotation. We suggest that this was how the head moved in life. The successive orientations and positions of the head in Text-figure 11 are traced from photographs taken during experiments with the model, whereas the successive positions of the tail are reasonable guesses.

The rearward protuberance of the k-, t- and f-spikes seems to help the spike to slide rearwards through the mud. It is functionally different from the anterior sharp protuberance of the spikes of *C. elizae*, which tended to prevent forward movement by pushing into sediment which the spikes otherwise slid over. The convex lower surfaces of the spikes allowed the spikes to sink into the sea bottom, rather than resting upon it.

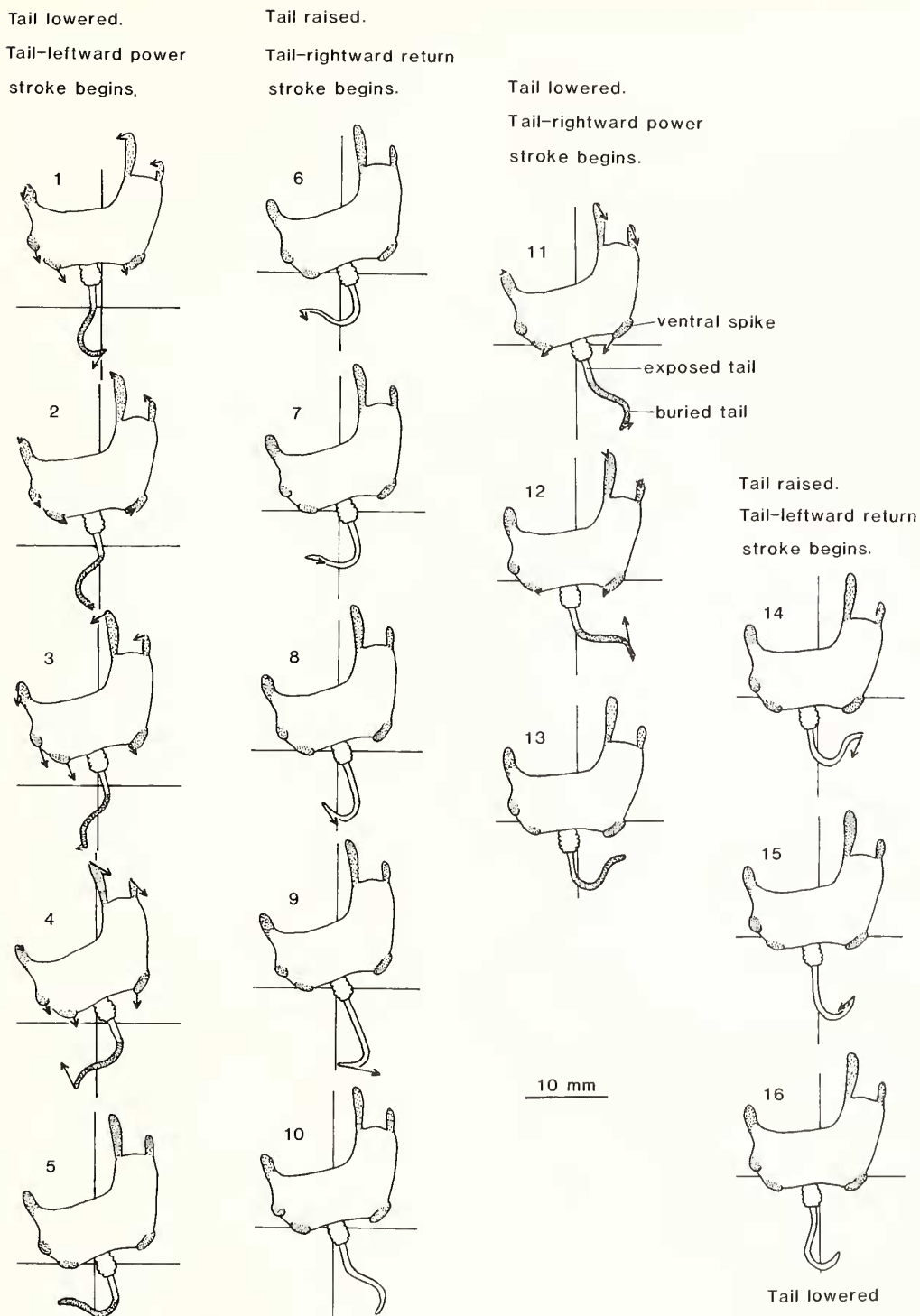
The locomotory cycle (Text-fig. 11) of *Procothurnocystis owensi*, like that of *Cothurnocystis elizae*, probably comprised four strokes: a tail-leftward power stroke, a tail-rightward return stroke, a tail-rightward power stroke, and a tail-leftward return stroke. Unlike *C. elizae*, however, the action of the fore-tail would be confined to raising the mid- and hind-tail out of the mud before a return stroke, and depressing it into the mud before a power stroke. Also the actual motor for locomotion would lie in the muscles of the hind-tail, flexing forwards and leftwards during the tail-leftward power stroke and forwards and rightwards during the tail-rightward power stroke. Force from the flexible part of the hind-tail would be applied to the head by pulling leftwards and rearwards, or rightwards and rearwards, on the distal end of the rigid proximal part of the hind-tail. This rigid part would act as a lever pulling on the head via the fore-tail. In transmitting forces generated by the hind-tail, the anterior part of the fore-tail would behave as a hinge with a horizontal axis, transmitting the horizontal components of force but not the vertical component.

The posture of the hind-tail in Text-figure 9/2 is like that in the only known specimen of '*Cothurnocystis*' *fellinensis* (Pl. 2, fig. 1), while that of Text-figure 9/12 is like that of the only known specimen of *Procothurnocystis owensi* (Pl. 1, figs 1-3). However, the locomotion of '*C.*' *fellinensis* must have differed considerably from that of *P. owensi* since the fore-tail of '*C.*' *fellinensis* looks to have been laterally flexible, the stylocone was not deeply inserted into the fore-tail, and there was no rigid proximal portion to the hind-tail.

As concerns phylogenetic polarity, the locomotion of *Procothurnocystis owensi* is probably advanced compared with that of *Cothurnocystis elizae* in several respects, namely:

1. Several features are unique to *P. owensi* among known cornutes and therefore probably represent the advanced condition in all cases. Such are the deep insertion of the stylocone into the fore-tail, the shallowness of the anterior excavation of the stylocone, the presumed small size of the fore-tail muscles, the more-than-double number of dorsal plates in the fore-tail, the presence of four ventral plates in the fifth ring of the fore-tail (rather than two), and the posterior protrusion of the ventral head spikes.

2. Predominantly dorso-ventral flexion of the fore-tail is not unique to *P. owensi*, for it elsewhere existed in the mitrates and in the most crownward plesions of the cornutes – namely those of *Reticulocarpos hanusi* Jefferies and Prokop, 1972, *Domfrontia pissotensis* (Chauvel and Nion, 1977) and *Prokopicystis mergli* Cripps, 1989. Lateral flexion of the fore-tail, however, is probably primitive for cornutes since it seems to have existed in most of the known species, and in particular in the two least crownward cornute plesions – those of *Ceratocystis perneri* Jaekel, 1900 and of



TEXT-FIG. 11. *Procothurnocystis owensi* gen. et sp. nov. Locomotory cycle, dorsal aspect; the scale bar refers to the fossil, not to the model (which was about $8\times$ larger); the spikes and the buried parts of the tail and appendages are stippled. 1-5, tail-leftward power stroke; 6-10, tail-rightward return stroke; 11-13, tail-rightward power stroke; 14-16, tail-leftward return stroke. The number of stages shown in each stroke is of no significance.

Protocystites menevensis Hicks, 1872. Also it probably existed in the solute *Dendrocystoides scoticus* Bather, 1913, and the solutes represent the paraphyletic group from which cornutes arose (Jefferies 1990). (The best evidence for lateral flexion in the fore-tails of these three animals is that the major plates of the fore-tail alternate with each other, and overlap each other, from right or left, in the ventral midline, and in *D. scoticus* in the dorsal midline as well.) All this suggests that dorso-ventral flexion of cornute fore-tails is advanced compared with lateral flexion. It is unlikely, however, that the dorso-ventral flexion of *P. owensi* is homologous with that of the crownward cornutes and mitrates, since the latter condition seems to have evolved in the chordate stem lineage between the plesions of *Hanusia* and *Reticulocarpus hanusi* (Cripps 1989a), and therefore much more crownward than *P. owensi*. Also the main motor in the locomotion of crownward cornutes, such as *R. hanusi*, lay in its primitive cornute and solute position in the muscles of the fore-tail, not in those of the hind-tail.

3. Lateral flexion of the hind-tail is probably advanced compared with lateral rigidity, since the hind-tail seems to have been laterally rigid in the anti-crownward cornutes *Ceratocystis perneri* and *Protocystites menevensis* and was rigid in all directions in most solutes, including *D. scoticus*. So far as can be discerned, lateral flexibility of the hind-tail may be homologous in all the cornutes that show it. This conclusion is uncertain, however, since the phylogeny of the cornutes is not well known, except near the crownward and anti-crownward ends of the cornute part of the chordate stem group.

The peculiarities of locomotion in *Procothurnocystis owensi* were probably adaptations to a very soft floor – so soft that the head sank into the mud down to the level of the ventral integument so that the spikes, much of the appendages and most of the tail were buried. A punting action, such as *Cothurnocystis elizae* probably used, will work only when the floor is strong enough to grip the end of the punt pole (or the downturned end of the hind-tail). This will mainly be true of sandy or silty sea floors, which do not appreciably weaken when stirred. Indeed, sands become stronger under pressure, so that the terminal hook of the hind-tail would grip the sea floor more firmly if it were deeply thrust into the sand than if inserted more shallowly. Clayey floors, on the other hand, because of thixotropy, lose nearly all their weak strength when stirred. On clayey floors, therefore, a swimming action will be more reliable than a punting action, for it will function even if the sediment loses all strength and becomes a viscous fluid.

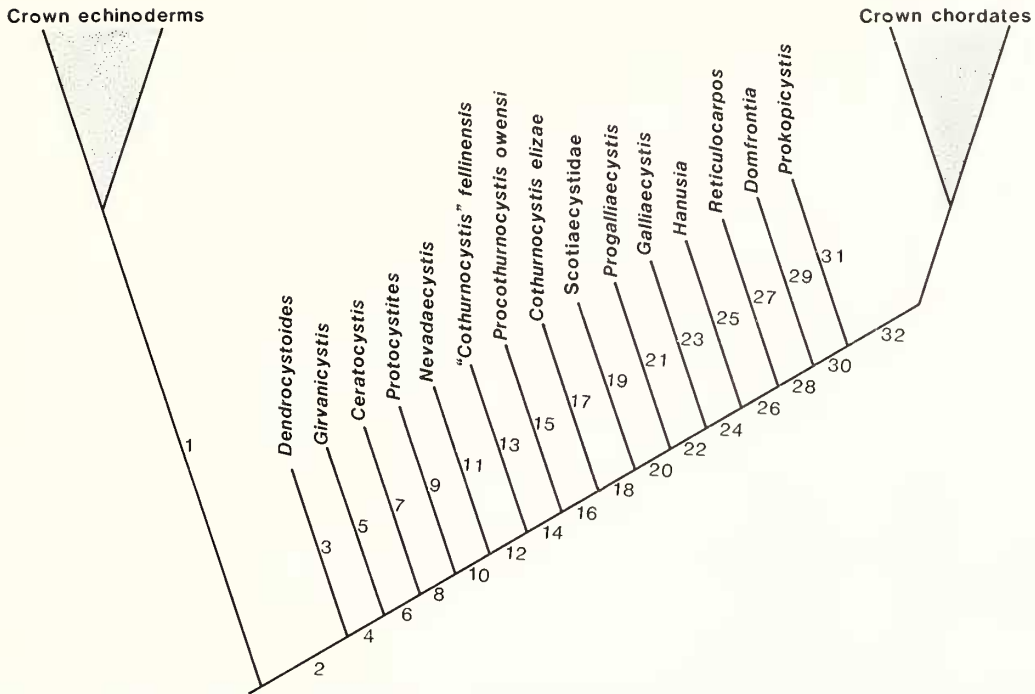
PHYLOGENETIC POSITION OF *PROCOTHURNOCYSTIS OWENSI*

Assuming the plesion series shown in Text-figure 12, then *P. owensi* represents a plesion intermediate between those of '*C.*' *fellinensis* and *C. elizae*. The relevant features of *P. owensi* can be analysed as follows:

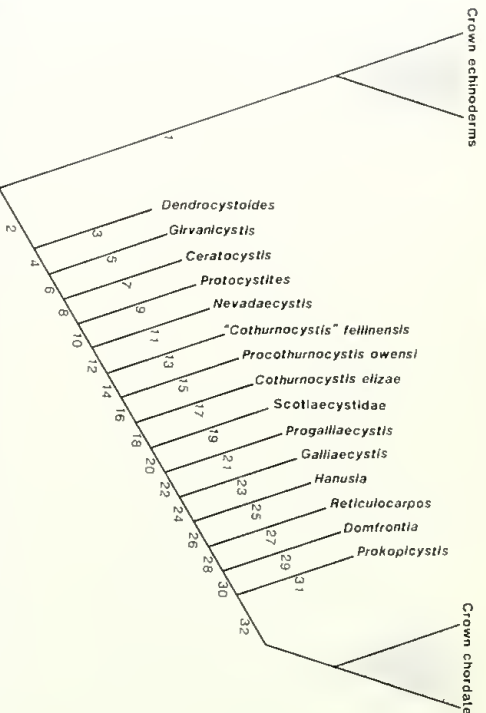
1. Evolutionary novelties which probably arose in the chordate stem lineage just anti-crownward of the plesion of *P. owensi* (between that plesion and the plesion of '*C.*' *fellinensis* in segment 14 of Text-fig. 12) are only two, namely: loss of the y plate and the contained median eye; and perhaps the reduction of the number of keel spines from six to three.

2. Autapomorphies of *P. owensi*, which would have arisen in segment 15 of Text-figure 12 are: the deeply inserted stylocone; more-than-doubling of the dorsal plates of the fore-tail; the leftward shift of the suture between the ventral plates of the 4th ring of the fore-tail; the increase in number of the ventral plates of the 5th fore-tail ring from two to four; and rearward protrusion of the ventral spikes.

3. Only four evolutionary novelties probably arose just crownward of *P. owensi*, in the chordate stem lineage between the plesion of *P. owensi* and that of *C. elizae*, in segment 16 of Text-figure 12. These are: loss of the x plate; an increase in the number of gill slits from nine to about sixteen; extension of the gill slit series rightwards, so that the gonopore–anus came to open into the outwash of the gill slits; and entire loss of the keel spines from the dorsal integument.



TEXT-FIG. 12. Cladogram of the Dexiothetica to show the relationship of crown-group chordates and crown-group echinoderms to stem-group chordates. Among the latter, two solute plesions are shown (*Dendrocystoides* and *Girvanicystis*) and all the known cornute plesions (*Ceratocystis* to *Prokopicystis*). The numbered segments correspond to evolutionary novelties as follows: 1, echinoderm autapomorphics, e.g. loss of tail, loss of gill slit, sessility, quinquaradial symmetry, mouth in centre of upper surface etc.; 2, tripartition of tail, origin of notochord and brain, gill slit migrates to posterior left position on head; 3, antibrachial process; 4, dorsal plates of head large, complete marginal hinge line; 5, no known changes; 6, solute-cornute transition with loss of arm, loss of water vascular system, migration of hydropore to posterior right of head, migration of gonad, gonopore, and heart to posterior right of head, multiplication of gill slits, paired dorsal plates on hind-tail, stylocone, etc.; 7, no known changes; 8, dorsal surface of head flexible, gonopore-anus left of tail, plate wax divides into w, a and x; 9, very light construction of skeleton; 10, anterior U-plates of gill slits, origin of strut (as thickening of head floor), increased flexibility of dorsal surface of head, plate d included in frame; 11, lateral spread of e-spike and f-spike; 12, ventral surface of head flexible (except for strut), spines on dorsal keels, t plate in frame; 13, no known changes; 14, loss of plate y; 15, autapomorphies of *Procothurnocystis owensi*, such as deep insertion of stylocone in fore-tail, reduction of fore-tail muscles, posterior protuberance of l-, k- and t-spikes; 16, loss of keel spines, loss of plate x, increase in number of gill slits to about 16, extension of gill-slit row anterior to the gonopore-anus; 17, no known changes; 18, loss of plate t, approximate symmetry of plates h and i, overlap of fore-tail plates epsilon and theta over head plates g and j; 19, scotiaecystid autapomorphies, e.g. plate s, interbranchial elements; 20, loss of specialized branchial skeleton and specialized oral skeleton, acquisition of dorsal bar, reduction in length of l-appendage to form an l-spike, horizontal suture between anterior strut plate (m) and a; 21, no known changes; 22, further reduction of l-spike; 23, no known changes; 24, reduction of left side of head to produce a more symmetrical outline, visible distinction between prosencephalon and deuterocephalon; 25, autapomorphies of the genus *Hanusia*, including large plate in dorsal integument, C-shaped section of marginal plates, ribs on l-spike; 26, symmetrical outline for the head, flat ventral surface without spikes or appendages, very small size, abbreviated hind-tail with large spikes on the ossicles and stylocone, peripheral flange, very light histology of skeleton, separation of anterior strut plate from the frame; 27, large depressions in frame for transpharyngeal eyes; 28, ventral convexity of head, dorsal extensions of marginal plates towards the centre of the head, very large plates in dorsal integument, loss of anterior strut plate (m), shield-like expansion of h and i; 29, loss of dorsal bar; 30, strong expansion of tail plates epsilon and theta over plates g and j of the head, gonopore-anus opening into branchial region, loss of major dorsal plates of fore-tail; 31, absence of all but one dorsal integument plate behind the dorsal bar; 32, changes at cornute-mitrate transition including origin of right gill slits, origin of left and right atria, further expansion of epsilon and theta to form part of the head, loss of plates g and j, loss of cornute mid- and hind-tail by autotomy, regionation of mitrate fore-, mid- and hind-tail, origin of inner layer of ventral skeleton, etc.



TEXT-FIG. 12. Cladogram of the Devotheitic to show the relationship of crown-group chordates and crown-group echinoderms to stem-group chordates. Among the latter, two soluble plesions are shown (*Dendrocystoides* and *Girvanicystis*) and all the known cornute plesions (*Ceratocystis* to *Prapakcystis*). The numbered segments correspond to evolutionary novelties as follows: 1, echinoderm autapomorphies, e.g. loss of tail, loss of gill slit, sessility, quinquaradial symmetry, mouth in centre of upper surface etc.; 2, tripartition of tail, origin of notochord and bran. gill slit migrates to posterior left position on head; 3, antibrachial process; 4, dorsal plates of head large, complete marginal hinge line; 5, no known changes; 6, soluble-cornute transition with loss of arm, loss of water vascular system, migration of hydropore to posterior right of head, migration of gonad, gonopore, and heart to posterior right of head, multiplication of gill slits, paired dorsal plates on hand-tail, stylocone, etc.; 7, no known changes; 8, dorsal surface of head flexible, gonopore-anus left of tail, plate wax divides into w. and s.; 9, very light construction of skeleton; 10, anterior U-plates of gill slits, origin of strut (as thickening of head floor), increased flexibility of dorsal surface of head, plate d included in frame; 11, lateral spread of c-spine and f-spine; 12, ventral surface of head flexible (except for strut), spines on dorsal keels; 13, plate in frame; 14, loss of plate y; 15, autapomorphies of *Procothurnocystis owensii*, such as deep insertion of stylocone in fore-tail, reduction of fore-tail muscles, posterior protuberance of f-, k- and f-spines; 16, loss of keel spines; loss of plate x, increase in number of gill slits to about 16, extension of gill-slit row anterior to the gonopore-anus; 17, no known changes; 18, loss of plate i, approximate symmetry of plate h and i, overlap of fore-tail plates epson and theta over head plates g and j; 19, scutiaecystid autapomorphies, e.g. plate s, interbranchial elements; 20, loss of specialized branchial skeleton and specialized oral skeleton, acquisition of dorsal bar, reduction in length of l-appendage to form an f-spine, horizontal suture between anterior strut plate (m) and a; 21, no known changes; 22, further reduction of f-spine; 23, no known changes; 24, reduction of left side of head to produce a more symmetrical outline, visible distinction between proencephalon and deuterecephalon; 25, autapomorphies of the genus *Hanusia*, including large plate in dorsal integument, C-shaped section of marginal plates, ribs on f-spine; 26, ventral convexity of head, dorsal fat ventral surface without spikes or appendages, very small size, abbreviated hand-tail with large spikes on the ossicles and stylocone, peripheral flange, very light histology of skeleton, separation of anterior strut plate from the frame; 27, large depressions in frame for transphyaryngeal eyes; 28, ventral convexity of head, dorsal extensions of marginal plates towards the centre of the head, very large plates in dorsal integument, loss of anterior strut plate (m), shield-like expansion of h and i; 29, loss of dorsal bar; 30, strong expansion of tail plates epson and theta over plates g and j of the head, gonopore-anus opening into branchial region, loss of major dorsal plates of fore-tail; 31, absence of all but one dorsal integument plate behind the dorsal bar; 32, changes at cornute-mitrate transition including origin of right gill slits, origin of left and right arra, further expansion of epson and theta to form part of the head, loss of plates g and j, loss of cornute mid- and hand-tail by autotomy, regeneration of mitrate fore-, mid- and hand-tail, origin of inner layer of ventral skeleton, etc.